Homology thinking reconciles the conceptual conflict between typological and population thinking

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Abstract

This paper attempts to reconcile the conceptual conflict between typological and population thinking to provide a philosophical foundation for extended evolutionary synthesis (EES). Typological thinking has been considered a pre-Darwinian, essentialist dogma incompatible with population thinking, which is the core notion of Darwinism. More recent philosophical and historical studies suggest that a non-essentialist form of typology (i.e., representational typology) has some advantages in the study of evolutionary biology. However, even if we adopt such an epistemological interpretation of typological thinking, there still remains an epistemological and methodological conflict between these two styles of thinking. How can we relate typological thinking with population thinking in pursuit of more integrated or interconnected research into evolutionary biology? I propose that homology thinking, which is another style of thinking that recognizes homologous characters, provides a common basis for typological representations of character states and for character dynamics in an evolving population. Good examples of this bridging role are found in teratology and breeding, where variation and novelty are recognized in developmental and morphological traits, gene expression patterns, and so on. Essentialism-free, dynamic views of homology have great potential to reconcile typological and population thinking and to set the stage for the EES.

Key words: extended evolutionary synthesis (EES), evolutionary developmental biology (Evo-Devo), teratology, breeding, variation, novelty.

1. Introduction

It is widely accepted that developmental biology and morphology have been excluded from the evolutionary synthesis (ES) or modern synthesis, and have contributed much less to the ES (Churchill 1980; Coleman 1980; Ghiselin 1980, 2006; Hamburger 1980; Amundson 2005; Laubichler and Maienschein 2007). This exclusion has often been attributed to a conceptual gap between typological and population thinking (Mayr 1959a, 1959b; Mayr 1980; Ghiselin 1980; Amundson 2005). On the one hand, developmental biology and morphology appeal to various "types" in their explanations. For example, idealistic morphologists, such as Owen (1848), postulated idealized typical forms (i.e., "archetypes") of body parts. On the other hand, Darwinism and population genetics, which occupy the theoretical core of the ES, are based on the notion that the evolutionary unit is a population, and that evolution can be explained by trans-generational changes, mainly generated by genetic factors, in the population.

The relationship between these two styles of thinking was first formulated as an unavoidable conflict between two metaphysical views (Mayr 1959b). Recently, some historical and philosophical studies have argued against this formulation (Levit and Meister 2006; Lewens 2009a, 2009b; Love 2009). According to them, typological thinking does not have to be metaphysical; it can be, and historically has often been, a methodological tool, which can contribute to certain kinds of biological research without involving a problematic metaphysics. I agree with these authors that typological thinking does not have to be metaphysical and that it is more fruitful to interpret typological thinking from an epistemological and/or methodological viewpoint. However, I point out that even at the epistemological and methodological level, there is a gap between population and typological thinking: typological thinking ignores variation within a taxon by idealizing characters as discrete states, whereas variation is essential for population thinking to explain character dynamics. This gap can be an obstacle to recent attempts at an extended evolutionary synthesis (EES) or a new synthesis inclusive of evolutionary developmental biology (Evo-Devo) (Laland et al. 2015; Laubichler and Maienschein 2007; Pigliucci and Müller 2010). Although the two styles of thinking are meaningfully used within distinctive areas of evolutionary research, if we aim to integrate or interconnect these areas in a more comprehensive way, the gap between the two styles of thinking needs to at least be bridged.[1]

In this paper, I examine if it is possible to bridge the gap between typological and population thinking with "homology thinking." This style of thinking was proposed by Ereshefsky (2012) as a way to understand biological phenomena by focusing on the historical nature of homologues. Wagner (2016) made much of this idea and considered it as the third leg of the "three-legged stool of evolutionary biology," with the other two legs being population thinking and tree thinking (the latter style of thinking was proposed by O'Hara [1997] and recognizes that species are interconnected in an evolutionary tree).

To accomplish this goal, after characterizing typological, population, and homology thinking (Section 2), I evaluate the epistemological advantages and disadvantages of typological and population thinking in macro/mega- and micro-evolutionary scales with an examination of how the notion of homology contributes to explanations in each case (Sections 3 and 4, respectively). Typological thinking often has greater explanatory power than population thinking in the macro- and mega-evolutionary scales because of the lack of population traceability, whereas population thinking dominates the micro-evolutionary scale. I also point out that the approaches of modern molecular biology, including those adopted in developmental biology and Evo-Devo, have a methodological affinity to typological thinking. Then I discuss how typological and population thinking can fruitfully be mediated by

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[1] Here "the gap is bridged" does not mean that the gap is completely filled or closed but that the two areas separated by the gap can be interrelated, although the gap remains.

homology thinking, with reference to studies of teratology and breeding as examples (Section 5). Finally, I examine the philosophical status of homology thinking and explore possible methods to bridge typological and population thinking at the epistemological level (Section 6). For the purpose of this conceptual bridging, it is crucial to recognize the dynamic aspects of homology. I thus introduce a recently proposed homology concept that highlights its dynamicity (Suzuki and Tanaka 2017) and suggest that such dynamic views of homology have the potential to bridge the gap between typological and population thinking and to set the stage for a new evolutionary synthesis.

2. Type, population, and homology: Styles of thinking in biology

Biologists and philosophers have characterized and discussed several "styles of thinking" in biology, each of which is a specific way to view the living world. Different styles of thinking recognize or highlight different aspects of biological phenomena. They are often associated with different sets of observational, experimental, and representational practices, as well as with different research fields. In this section, I first describe two such styles of thinking (typological and population thinking), with a focus on how previous studies have formulated the relationship between them. Then, I introduce and characterize homology thinking, which is another style of thinking that operates in the field of evolutionary biology.

Ernst Mayr, in the 1950s, formulated the concepts of typological thinking and population thinking, which according to him, are fundamentally incompatible (Amundsen 2005; Chung 2003; Mayr 1959b). He originally treated this dichotomy only in a taxonomic context (pre-Darwinian species fixists versus neo-Darwinists), but eventually elevated it to being the major problem in all biological disciplines, and then in the entire history of Western thought (Amundsen 2005, 205). According to Mayr, typological thinking sees "a limited number of fixed, unchangeable 'ideas' underlying the observed variability" and hence conceives the natural world by classifying things into discrete categories (Mayr 1959a, 2). This style of thinking is in sharp contrast with population thinking, which recognizes the uniqueness of individuals in the world:

> "All organisms and organic phenomena are composed of unique features and can be described collectively only in statistical terms. Individuals, or any kind of organic entities, form populations of which we can determine the arithmetic mean and statistics of variation. Averages are merely statistical abstractions, only the individuals of which the populations are composed have reality. The ultimate conclusions of the population thinker and of the typologist are precisely the opposite. For the typologist, the type (*eidos*) is real and the variation an illusion, while for the populationist the type (average) is an abstraction and only the variation is real. No two ways of looking at nature could be more different." (Mayr 1959a, 2)

Mayr argues that this incompatibility between the two metaphysics is the reason why embryology or developmental biology was excluded from the ES; population thinking is the basic metaphysics of the ES. Evolution is understood as a change in the frequencies of an allele in a population. By contrast, the study of biological development relies on typologist metaphysics, and hence cannot be integrated into the theoretical and conceptual framework of the ES (Mayr 1980).

Recently, several historical and philosophical studies have pointed out problems in Mayr's formulation of the conflict between the two styles of thinking (Levit and Meister 2006; Lewens 2009a, 2009b; Love 2009; Winsor 2006). An idea that is shared by some of those studies is that typological thinking does not have to be and has not always been metaphysical. For example, Levit and Meister (2006) examined some idealistic morphological theories. According to them, typology was a conceptual tool for classification based on structural characters and had no necessary connection with a problematic metaphysical view of life, such as essentialism or species fixism, which Mayr wrongly associated with typology. Love (2009) pursued a similar idea by taking a philosophical approach. Viewed from an epistemological perspective, typological thinking plays a crucial role in scientific practice by facilitating various activities through idealization and approximation. Love (2009) encouraged a reconfiguration of typology in terms of scientific practice or epistemology, instead of metaphysics, to appreciate the importance of typology.

I share with these authors the view that it is more fruitful to interpret typological thinking in terms of epistemology. However, even if we shift our attention from metaphysics to epistemology, the question remains of how to integrate studies based on these two different styles of thinking. The two styles of thinking are suitable for investigating different evolutionary timescales; while population thinking traces changes in allele frequencies in a population at the micro-evolutionary scale, typological thinking idealizes discrete character states that emerge through macro/mega-evolutionary processes. If the EES aims to provide a comprehensive picture of evolution involving different evolutionary timescales, the two styles of thinking must be mediated or bridged (see Sections 3 & 4).

Another style of thinking that we discuss here is homology thinking. Although the notion of homology has a deep historical root, it is only in the last decade that the notion has been discussed as a particular style of thinking that parallels typological and population thinking. Ereshefsky (2012) characterized homology thinking as an approach of historical explanation, which accounts for a certain character by referring to its history. Following this characterization, Wagner (2016) proposed that homology thinking consists of three insights: multicellular organisms are composed of sub-systems, which are developmentally individualized; those sub-systems can change independently via evolutionary processes; and those sub-systems are indirectly inherited and constitute lineages. Therefore, homology thinking focuses on developmentally and evolutionarily quasi-independent sub-systems (i.e., modules) of an organism and explains their properties by referring to their histories.

It is notable that Ereshefsky (2012) and Wagner (2016) stressed different (but non-exclusive) aspects of homology thinking; the former highlighted the historical continuity of a character, while the latter underscored its dynamics and mechanisms in evolutionary and developmental processes. In this paper, I simply and minimally characterize homology thinking as "recognition of the sameness of a character (both between different organisms and within an organism)." In other words, it is the art of identifying characters in different contexts. Here the two aforementioned views can be regarded as being based on different grounds for "sameness:" one on historical continuity and the other on dynamics and mechanisms.[2] Recognition of homologs can be given without assumption of any "type," and without consideration of any population (for example, see the below mentioned case of identifying homologous characters in fossils). Thus, homology thinking is essentially independent of typological and population thinking. On the contrary, it provides a crucial basis for these two ways of thinking and bridges the gap between them as discussed below.

3. Macro/mega-evolution

In this and the next section, I discuss how the different styles of thinking contribute to different aspects of evolutionary research. I point out the following difference: typological thinking plays a significant role in the study of macro- and mega-evolution; population thinking serves as the basis of the study of micro-evolution; and homology thinking facilitates research in both contexts. First, let us define micro-, macro- and mega-evolution.

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[2] Note that these "grounds" do not necessarily provide certain criteria for the identification of homologs. We can recognize homologs, even if neither their historical continuity nor developmental mechanism is clear. See Remane (1952) for the most prominent operational criteria of homology (summarized in Griffiths 2007, 648).

According to Dobzhansky (1937, 12), macro-evolutionary changes occur on geological time scales, while micro-evolutionary processes are observable within the span of a human lifetime (i.e., intra-specific). Thus, macro-evolution in Dobzhansky's sense can be applied to broad evolutionary scales, ranging from trans-specific to trans-phylar levels. The term mega-evolution was introduced by Simpson (1944), who referred to evolution at the larger scale (i.e., at the trans-phylar level) as a special case of macro-evolution (Simpson 1944, 98).[3]

Many researchers, including Dobzhansky, assume that macro-evolution can be explained by the same logic as micro-evolution. As Futuyma (1998, 477) wrote, "one of the most important tenets of the theory forged during the Evolutionary Synthesis" was that macro-evolutionary differences "arise from the accumulation of the same kinds of genetic differences that are found within species." I do not intend to refute this assumption. In fact, there is much paleontological evidence that demonstrates gradual changes in trans-specific and trans-generic evolution (i.e., macro-evolution sensu stricto) (Levinton 2001, Ch. 6). However, when we focus on larger evolutionary scales (particularly at the mega-evolutionary level), we actually face greater difficulty in tracing the population continuity than we do with micro-evolution. This difficulty appears to be derived from the incompleteness of the sedimentary and fossil records (Levinton 2001, 365). That is, even if it is *theoretically* possible, it is *practically* difficult to know the population dynamics and thus to adopt population thinking at larger scales. Therefore, the explanatory power of population thinking becomes more limited at these scales.

Instead of population thinking, homology plays a more important explanatory role here. Particularly at the mega-evolutionary level, identifying homologous characters bridges the gaps between different geological times and provides crucial clues to reconstruct the

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[3] It is notable that Simpson (1944, 98) argued that "the paleontologist has more reason to believe in a qualitative distinction between macro-evolution and mega-evolution than in one between micro-evolution and macro-evolution."

evolutionary history. For example, the presence of the notochord, gill slits (or gill pouches), and vertebral elements are considered markers of vertebrates, for which the evolutionary continuity of the earliest fossils has huge gaps and is not traceable at all (e.g., *Haikouichthys*, Shu et al., 2003; *Metaspriggina*, Conway Morris and Caron 2014; Tully monster *Tullimonstrum*, McCoy et al. 2016). On the contrary, the existence of homologous characters suggests evolutionary continuity from these ancestral lineages to their recent relatives. Furthermore, the identification of homologs in a fossil does not necessarily require typological thinking (abstraction, generalization, idealization, or approximation), although this way of thinking is required for reconstruction and schematic illustration of these fossil animals (see below).

Even at smaller scales (macro-evolution sensu stricto, such as trans-specific and trans-generic levels), we often track certain homologous characters to reconstruct the evolutionary changes. For example, in the evolution of horses, where it is shown that the digits were gradually degenerated, we identify the homologous digits in different species and then figure out which digits were degenerated or conserved (Solounias et al. 2018, and literature cited within).

Typological thinking also plays an important role at macro- and mega-evolutionary scales. For example, we often schematically represent morphological characters as discrete types to recognize general features shared across taxa (such as the ground plan of the tetrapod limb). Such *representational typology* is found broadly in biology in general (e.g., protein domains, modes of locomotion, and developmental stages) (Love 2009). As Love (2009) argued, typological thinking can be understood as a scientific tactic to represent natural phenomena using idealizations and approximations. The use of typology to represent natural phenomena with abstraction and generalization facilitates explanation, investigation, and theorizing in different research fields of biology.

In summary, the explanatory power of population thinking is limited at the macro- and mega-evolutionary scales. Homology and typological thinking are more effective at such geological timescales because of the limitation of population traceability.

4. Micro-evolution

In contrast to the case of macro- and mega-evolution, population thinking has overwhelming explanatory power at the micro-evolutionary scale, where populations are continuously traceable. By quantifying statistical parameters, such as population size and phenotypic variance, evolutionary biologists are able to evaluate the effects of natural selection, genetic drift, and so on (reviewed in Saccheri and Hanski 2008). Homology thinking also plays an important role in these studies. When researchers focus on a certain character of interest and trace its evolutionary trajectory, they need to be able to identify the homologous character in various individuals. For example, in the case of beak evolution in Darwin's finches (Grant and Grant 2002), the beaks must be identified consistently as homologs. Although some may consider this a truism, these researchers successfully identify homologs in different organisms. In fact, misidentification sometimes happens, especially when focusing on a character that is seemingly homologous but in fact homoplastic as a result of convergence or parallelism. From this point of view, these researchers certainly exercise homology thinking, whether or not they are aware of it. Therefore, the notion of homology is a prerequisite for studying character dynamics at a micro-evolutionary scale. Here we find a clue as to how to bridge the gap between typological and population thinking at the micro-evolutionary scale (see Section 4).

On the other hand, typological thinking is less explanatory at micro-evolutionary scales. Typological thinking necessarily filters out variation in a population to abstract a type and hence fails to recognize gradual evolutionary changes. A significant form of variation filtering is genetic standardization of experimental organisms; experimental genetics and molecular biology often establish “pure lines” or “inbred lines” of their experimental organisms to make the genetic background as identical as possible (Ankeny and Leonelli 2011). Genetic variation is considered noise here because they could mask the experimental effect. Some Evo-Devo researchers also rely on the use of standardized organisms and hence have the tendency to overlook variation. For example, when they compare developmental traits or expression patterns of homologous genes between two species, they tend to compare averages of the traits or expression patterns. Let us consider an imaginary case of a researcher who focuses on the contribution of gene X to the development of a morphological trait Y and asks whether or not expression of X in the development of Y is conserved in vertebrates or not. For this purpose, the researcher might use several model organisms, such as the mouse, chick, *Xenopus*, and zebrafish, and examine the expression patterns of X in these animals. In such a case, varieties within each species are ignored, and the species under research are treated as types instead of as variable populations. Furthermore, expression patterns are often represented as schematic illustrations, which can be considered typical examples of representational typology.

Nonetheless, this statistical type does not necessarily presuppose typological thinking in an essentialist sense; it can be a statistical “modality descriptor” (Levinton 2001, 13), which is not real and has no causal efficacy (sensu Sober 1980), but rather represents a modal form of a population. However, even if it is metaphysically non-problematic, variation-filtering poses an epistemological and methodological issue because typological and population thinking fundamentally differ in how they treat variation; the former ignores it, whereas to the latter, variation is the most crucial part of evolutionary processes. This difference makes it difficult to mediate the two styles of thinking to acquire a more comprehensive picture of evolution by combining results and approaches from various fields, some of which rely heavily on typological thinking (i.e., developmental biology, morphology, and paleontology) and others of which are based mainly on population thinking (i.e., population genetics).

5. Bridging the gap: teratology and breeding

An epistemological and methodological problem that prevents us from establishing an EES is that molecular developmental biology tends to filter out variation in a population of model organisms. To bridge the gap between typological thinking and population thinking, it is crucial to reconcile considerations of those features that are highlighted by the former (e.g., character identities and novelties) and those highlighted by the latter (e.g., variation). We can find hints of such bridging in studies of teratology focusing on developmental and morphological variation that might lead to evolutionary novelties (see Guinard 2012, 2015). Such studies involve both typological and population thinking to elucidate how a novel character emerges from variation in a population. Furthermore, homology thinking serves as a conceptual mediator between the two styles of thinking.

Let us consider the teratology of polydactyly as an example. Polydactyly is hand/foot malformation caused by digit duplication and presents several patterns: radial (prefixal), ulnar (postaxial), and central polydactyly (Farrugia and Calleja-Agius 2016). Radial polydactyly is the most common form (Crick et al. 2003), in which the extra digits appear anterior to the pollex (thumb) or the hallux (the thumb-toe). Although in most breeds of dogs the hallux is vestigial (the “dewclaw”) or even absent (particularly in small dogs), an extra (sixth) toe tends to appear (the “double-clawed” condition) in some breeds, such as the St. Bernard and Newfoundland, and is even a standard (i.e., artificially selected) for the Great Pyrenees and Norwegian Lundehund (Alberch 1985; Kropatsch et al. 2015). This sixth toe may have some adaptive advantages, such as for swimming, working through deep snow, or preventing dogs from slipping off rocks (Prentis 1906; Galis et al. 2001; Kropatsch et al. 2015). However, mutations for polydactyly are likely to have negative pleiotropic effects to other body parts and cause high mortality rates (Bonnet et al. 1997; Galis 2001), explaining why the sixth toe is not common in most dog breeds. Alberch (1985) proposed an alternative hypothesis, based on experiments in amphibians (Alberch and Gale 1983, 1985): larger breeds have a greater number of cells in the limb bud, which can produce an extra digit; smaller breeds have a smaller limb bud and hence lack a hallux. Indeed, the prepollex and prehallux (the extra skeletal elements anterior to the pollex and hallux, respectively) are observed in many frogs, although there is controversy on whether these are true digits or not, that is, whether there is serial homology between the extra digits and the other digits (Fabrezi 2001; Hayashi et al. 2015). Fabrezi (2001) examined the prepollex and prehallux in various anuran (i.e., frog) species and discussed the homology, variation, and evolution of them (see also Tokita & Iwai 2010). An enlarged distal prehallical element is closely related to burrowing or fossorial habits and appears in several taxa (Fabrezi 2001, 244), indicating that it has some adaptive advantages. If this is true, we can infer that an extra digit is formed as a morphological variation in a certain generation, and then its homologs spread throughout a population on a micro-evolutionary scale.

Population, homology, and typological thinking all operate in the research of polydactyly. Polydactyly is found as variation in some populations of several tetrapod taxa and has been under natural, as well as artificial, selection. At the same time, morphological states are regarded and represented as discrete types (e.g., Fabrezi 2001, Fig. 12 and 13). The extra digits formed by polydactyly are also distinguished from other digits and discussed in terms of their phylogenetic homology (among several lineages) and serial homology (between extra digits and the other digits). Here we see that the notion of homology mediates the typological and population thinking. Discrete types of morphological states are given an explicit evolutionary meaning by the recognition of homologous relationships within or between those types, while population thinking needs to recognize homologous characters prior to discussing their variation.

Let us imagine the case of prepollex evolution in frogs by comparing a population without (Frog A) and that with (Frog B) a prepollex (Fig. 1). At a glance, it seems that Frog A has four digits (as do most frogs), and Frog B has five digits, in the forelimb. It is unclear which digit in Frog A corresponds to which digit in Frog B (Fig. 1A, left). By careful examination (of anatomical elements, for example) via homology thinking, we can determine the digit homology, determining that there are skeletal elements of the prepollex in both Frog A and Frog B, although these parts are not outwardly visible in Frog A (Fig. 1A, right). Based on this homology and through typological thinking, we can then idealize the structure and illustrate it by schematic representation, where variations in each animal group are abstracted (Fig. 1B). At the same time, we are also able to hypothesize the character dynamics in frog populations through population thinking. For example, it is possible to assume that there were variations in an ancestral population, whereby some individuals (X*) possessed an obvious prepollex, while others (X) did not, and Frog B and Frog A are descendants of X* and X, respectively (Fig. 1C). We can test this hypothesis by examining detailed fossil records, as illustrated in the case of horse digits described above.

[**Fig. 1** Bridging role of homology thinking between typological and population thinking.]

Breeding is another example allowing coexistence of the three ways of thinking. Although I pointed out a negative epistemological aspect of inbreeding (variation filtering, see Section 4), breeding in general can be a good experimental model of evolution. Charles Darwin, in *On the Origin of Species*, presented his evolutionary theory with an analogy between artificial and natural selection (Darwin 1859; Gayon 1998; Sterrett 2002). Some Evo-Devo researchers are studying evolutionary novelties using domestic breeds. For example, Ota and his colleagues (Abe et al. 2014; Ota and Abe 2016, Fig. 9) have revealed developmental mechanisms underlying the formation of twin-tail morphology in goldfish. They suggested that attractive and valuable ornamental morphologies such as the twin-tail have been the subject of strong directional selection, and the most preferred phenotypes are fixed by stabilizing selection. A similar evolutionary process can occur under natural selection as well, when a phenotypic variation is strongly advantageous in a certain environment. Recognizing homology is also important in tracing these processes; it enables us to identify whether the phenotype evolved once (homology) or more than once (convergence, parallel evolution, or homoplasy). Moreover, the states of single- and twin-tail are often illustrated as discrete representational types.

Variation-oriented morphological studies such as teratology and breeding can be a "buffer zone" between typological and population thinking, and the notion of homology can mediate them as a "bridge" or "hinge" (Fig. 1). Unlike typical cases of morphology or molecular developmental biology, these studies focus on variation in homologous characters, as does population genetics. At the same time, these studies enable us to recognize different morphological states as discrete types (e.g., polydactyly and twin-tail, as distinguished from the normal states). Homology thinking plays a bridging role here, providing a common basis for typological and population thinking by highlighting homologous characters.

One major reason why homology thinking can mediate typological and population thinking is that it applies across different timescales of evolution, i.e., it is *scale-free*. Although population thinking does play a predominant role at micro-evolutionary scales, its explanatory power becomes relatively week at macro- and mega-evolutionary scales. Conversely, typological thinking has epistemological advantages in studies of macro- and mega-evolution but has huge methodological weaknesses in the study of micro-evolution. Unlike these styles of thinking, homology thinking is not constrained by any specific scale of evolution. This is the key to mediate the other two styles of thinking: recognition of a homologous character is required both to trace character dynamics in a population during natural/artificial selection (population thinking) and to consider interestingly distinctive character states while making explicit their evolutionary meanings (representational version of typological thinking). The cases of polydactyly and breeding described above illustrate these functions of homology thinking.

6. Rethinking homology thinking

Although homology thinking can be a linchpin of typological and population thinking, we still need to examine what kind of homology concept is appropriate for this role. The ontological status of homology, in particular whether a homolog is a member of a natural kind or a part of an individual, has been a matter of intense debate (e.g., Assis and Brigandt 2009; Ereshefsky 2009, 2010b; Suzuki and Tanaka 2017; Wagner 2014). It can be argued that homologs are members of a natural kind, which share essential properties or similar sets of properties (a homeostatic property cluster or HPC) (Assis and Brigandt 2009; Brigandt 2007, 2009). On the other hand, homologs can be considered parts of an individual (i.e., a species as an ontological individual) that are historically connected rather than having any shared properties (Ereshefsky 2009, 228; Ghiselin 2005, 95). This controversy of individual versus natural kind first took place with respect to the problem of species (Ereshefsky 2007, 2010a), where typological thinking and essentialism are often viewed as synonymous labels for a problematic way to comprehend species, which fails to comport with Darwinian evolutionary theory (see Amundson 2005; Brigandt 2017; Winsor 2006).

Some authors have argued that a homolog can be construed as *both* a part of an individual *and* a member of a natural kind (e.g., Assis and Brigandt 2009; Brigandt 2009, 2017), and they emphasize epistemological advantages (explanatory roles) of their view. As Evo-Devo research has focused much more on the developmental mechanisms of homologs, the idea of developmental type (including homology) as a natural kind has become reputable (Brigandt 2017; Wagner 2014; Rieppel 2005). This was made possible in part because, unlike the traditional natural kind view, new versions of the natural kind view allow some variability of properties that characterize a particular homolog. For example, the HPC view characterizes a homolog in terms of stable similarities based on a number of common properties, instead of strictly the same set of properties or essences. Thus, the natural kind view can accommodate evolutionary changes and variation in property clusters that characterize a homolog.

However, despite this modification, the natural kind view is not the best candidate for a concept of homology that serves to bridge typological and population thinking. Although theoretically the HPC view has room for changes and variation in property clusters, it still appears to have an inevitable tendency to filter out variation. This is because the focus of the HPC view is on the stability of property clusters: the view seeks a set of properties that are stably shared by instances of a homolog and also homeostatic basal mechanisms that are responsible for the stability. This specific focus may result in missing fluctuations, which can indeed be evolutionarily important.[4] Capturing dynamicity and variability of homologs is the key to mediating typological and population thinking in evolutionary biology. In the remainder of this section, I discuss a recently proposed homology concept that emphasizes the dynamic aspects of homology: the persistently reproducible module (PRM) view (Suzuki and Tanaka, 2017).

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[4] For other problems of this theory in the context of homology, see Suzuki and Tanaka (2017).

According to the PRM view, homologs are characterized as modules, persistently reproduced in evolutionary (i.e., reproduction) and developmental (i.e., regeneration) processes. For example, the eyes of a newt lineage are repetitively and persistently produced throughout generations, and the eyes in a newt can also be produced many times (Eguchi et al. 2011). As evolutionary and developmental homologs, the eyes show both individual and natural kind aspects. On the one hand, they are historical (i.e., spatiotemporally restricted) entities engaging in evolutionary and developmental processes in a manner similar to individuals. On the other hand, their repetitive generation enables us to attribute shared properties to them and to regard and represent them as of the same type. An important point here is that we do not need to assume essences or homeostatic properties with basal mechanisms for their formation. We can characterize a homolog in terms of repetitive and persistent production of a phenotype. The shared characters and their basal mechanisms can dynamically change.

Indeed, the developmental mechanism for a homologous character changes in many cases. This phenomenon is known as developmental systems drift (DSD) (Haag and True 2018; True and Haag 2001). For example, the neurulation mechanisms are significantly different between anamniotes (*Xenopus*), in which bone morphogenetic protein (BMP) signaling is necessary, and amniotes (chicks), in which there is no contribution of the BMP pathways. It is also notable that mechanisms underlying the formation of the same organ (homolog) are often different during development than during regeneration (Vervoort 2011), indicating that shared basal mechanisms are not requisite for the formation of homologs.

The PRM view can account for the homologous variation and novelty discussed in the previous section. For example, an extra digit can be considered a co-option of a digit module (see Suzuki and Tanaka 2017, Fig. 4). The homology of this extra digit is recognized if it is reproduced persistently through generations. Another example is the head spot of the Tancho (“red-cap”) variety of the colored carp (Koi) (Suzuki and Tanaka 2017, 176). In this variety, the red pigmentation is found only at the top of the head, while its ancestral variety Kohaku (“red and white”) exhibits red and white color patterns in the whole body (Axelrod 1988). Thus, the head spot of Tancho appears to have evolved by restriction of the red pigmentation to the top of the head, or at least its separation from other trunk pigmentations. A breeder might have recognized this phenotype and planned to fix it as a strain, then when it began to be reproduced persistently through generations as homologs, the Tancho variety was established.

Although the persistency of module reproduction is key to recognizing homologs, persistency itself is a matter of degree. How many times should modules be persistently reproduced to be recognized as homologs? At least genetic fixation appears to be necessary for the establishment of homologs as PRMs, excluding the possibility that the modules are formed coincidentally. The certainty of homology increases when the formation mechanisms underlying PRMs are conserved, but these mechanisms are not necessarily always the same or even similar, considering DSD. Therefore, I postulate that homologs are established with genetically fixed persistency, via underlying mechanisms that are dynamically changeable.

Another view of homology that accommodates a certain form of dynamicity is proposed by Otsuka (2017), who suggests that homology can be defined as causal graph isomorphism over lineages, or conservation of the underlying causal structure over evolutionary history.[5] This view contends that two mechanisms can be seen as homologous as long as their causal structures remain the same, even if the entities that constitute them differ. Although DSD seems to challenge this view, according to Otsuka, topological features of the causal network may remain invariant if the drift concerns only genetic or cellular materials (Otsuka 2017, 1136).

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[5] The relationship and compatibility between PRM and causal model views is worthy of further discussion. As this issue strays from the main topic in the current paper, however, it is left for future work.

For the purpose of bridging the gap between typological and population thinking, it is important to adopt a homology concept that highlights the dynamic aspects of homology.[6] Such a homology concept can provide a conceptual foundation to relate character dynamics in a population with discrete types of character states. Although further discussion is needed to conclude which homology concept is best suited for this role, the PRM view appears to be a good candidate.

7. Conclusion

This paper discusses how homology thinking can bridge typological and population thinking. Even if we reject the fundamental incompatibility between typological and population thinking formulated by Mayr (1959b) and recognize the epistemological advantages of typological thinking, the question remains of how to relate the two styles of thinking for the integration of different kinds of evolutionary studies. I argue that homology thinking can facilitate such bridging, with reference to significant cases in teratology and breeding as examples. The variation-oriented morphological studies in these areas can serve as a "buffer zone," where homology thinking provides a common basis for both tracing of character dynamics in a population over time and the evolutionary meaning of discrete types of character states. Homology thinking that highlights the dynamic aspects of homologs can promote productive cooperation between evolutionary and developmental biology and hence facilitate a more comprehensive understanding of evolution.

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[6] The processual philosophy of biology (Dupré and Nicholson 2018) is an ontological theory that has some affinity to a dynamic view of homology. According to the PRM view, for example, homologs are considered neither members of a natural kind nor parts of an individual but as subprocesses (each homolog) of a process (homologs as a whole) that exhibit coherence (modularity of each homolog) and persistence (persistent reproductivity of homologs). For a detailed discussion of coherence and persistence of biological processes, see DiFrisco (2018). Also, dispositionalism in the processual philosophy of biology might provide a better framework for understanding causation in biology, ontologically, and epistemically (Anjum and Mumford 2018).

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Conflict of interest

The author declares that he has no conflict of interest.

Availability of data and material

Not applicable.

Code availability

Not applicable

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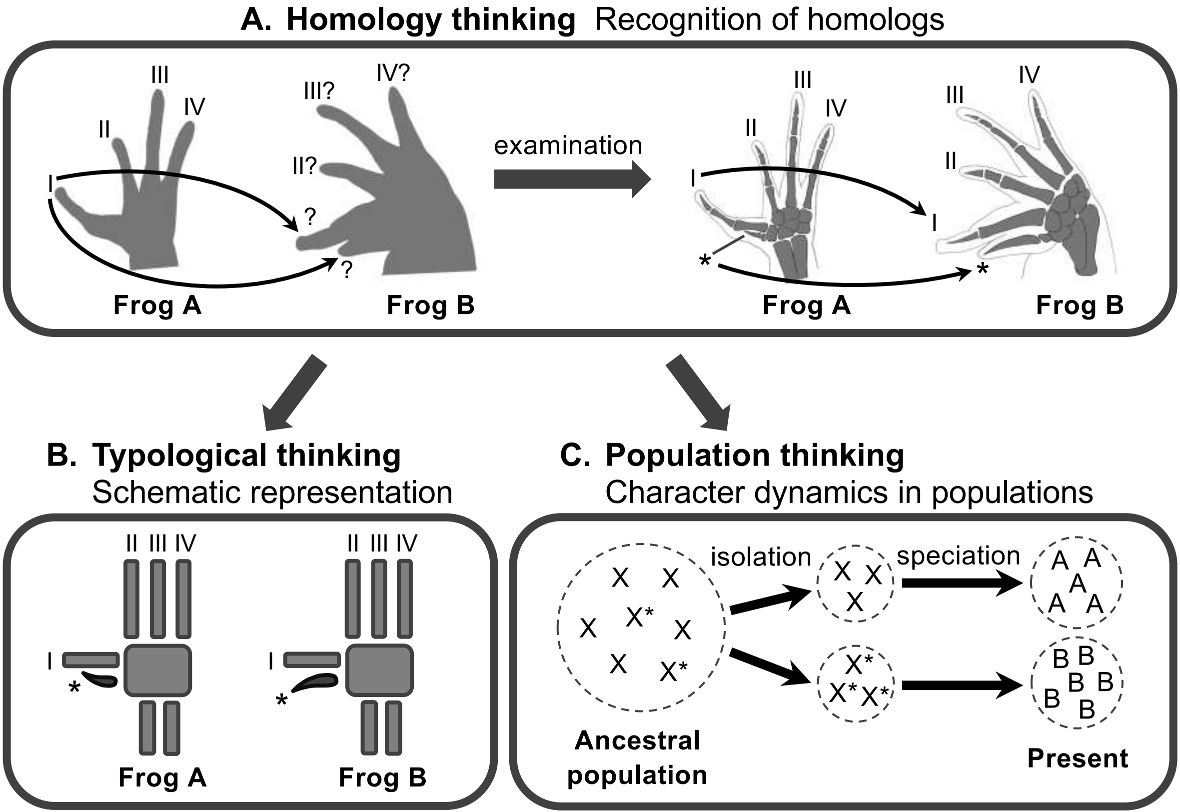
Figure legend

Fig. 1. Bridging role of homology thinking between typological and population thinking. (A) Homology thinking. (B) Typological thinking. (C) Population thinking. I, II, III, and IV indicate the 1st, 2nd, 3rd, and 4th digits, and * indicates the prepollex, respectively. See text for details. Illustrations are based on Tokita and Iwai (2010).


A. Homology thinking Recognition of homologs
III
IV
II
I
III?
IV?
II?
?
?
Frog A
Frog B
examination
III
IV
II
I
I
*
*
III
IV
II
Frog A
Frog B
B. Typological thinking
Schematic representation
II III IV
I
*
Frog A
II III IV
I
*
Frog B
C. Population thinking
Character dynamics in populations
X X X* X X X X*
isolation
X X X
X* X* X*
speciation
A A A A A
B B B B B B
Ancestral population
Present